

Very old patelliform gastropods from the Early Cambrian of China: Reconsideration of the systematic position of *Archaeotremaria*

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Abstract – *Archaeotremaria polytremata* Yu from the Lower Cambrian Maidiping Member of the Hongchunping Formation of Sichuan, China, was originally described as a primitive monoplacophoran. A restudy of the holotype and paratype has led to a reconsideration of its systematic position. *A. polytremata* has a patelliform shell with a series of median-dorsal tremata extending from the apex to the anterior margin and periodic rugae. The species is now reassigned to the Gastropoda, rather than Monoplacophora.

INTRODUCTION

The fossils redescribed and refigured in the present paper were collected by the writer and his colleagues in 1977 from the upper part of the Lower Cambrian Maidiping Member of the Hongchunping Formation. The section is situated at the west side of Gaoqiao village, about 14 km south of the city of Emei, Sichuan, China. The Maidiping Member is about 32 m in thickness; it is composed mainly of light to dark inequigranular arenaceous dolomites with collophane. The member conformably overlies the Precambrian Maoergang Member of the Hongchunping Formation and is overlain conformably by the Lower Cambrian Jiulaodong Formation (Yin *et al.* 1980) (Figure 1). The Maidiping Member is one of several units in the Yangtze region of China which are rich in micro-molluscan fossils. Specimens of *Archaeotremaria polytremata*, often occur together with interesting and characteristic forms of the Meishucun Stage, such as *Watsonella yunnanensis* (He and Yang), *Circotheca subcurvata* Yu, *Merismoconcha multisegmentata* Yu, *Maidipingoconus maidipingensis* (Yu) and *Yangtzeconus priscus* Yu. These fossils are widely distributed in eastern Yunnan, western Hubei and southwestern Shaanxi.

The patelliform fossil *Archaeotremaria polytremata* Yu, was described by the writer in 1979 as a member of the Class Monoplacophora. A restudy of the holotype and paratype has concentrated on some characters which previously were uncertain, such as the concentric periodic rugae, and a development of tremata throughout ontogeny. These observations provide the basis for reconsidering the systematic position of the genus.

Illustrated specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese

Academy of Sciences, Nanjing, People's Republic of China.

SYSTEMATIC PALAEOLOGY

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia Milne-Edwards, 1848

Order Archaeogastropoda Thiele, 1925

Suborder Bellerophontida Ulrich and Scofield,
1897

Superfamily Archaeotremarioidea Yu, 1979

Family Archaeotremariidae Yu, 1979
(= Granoconidae Yu, 1979)

Diagnosis

Shell minute to small, univalve, bilaterally symmetrical, patelliform, cyrtconic; with a series of tremata on the median dorsal side.

Remarks

The family Granoconidae Yu was established by the writer in 1979 p. 265, based on the genus *Granoconus* Yu, 1979. Subsequent detailed comparison demonstrated that *Granoconus* is quite similar to *Archaeotremaria* Yu, 1979: 249, especially in the dorsal tremata on tubular projections. For this reason, the genus *Granoconus* was relocated in the family Archaeotremariidae Yu, 1979 by the writer in 1987. It follows therefore that the family Granoconidae should be considered a junior synonym of the family Archaeotremariidae (Yu, 1987b: 170).

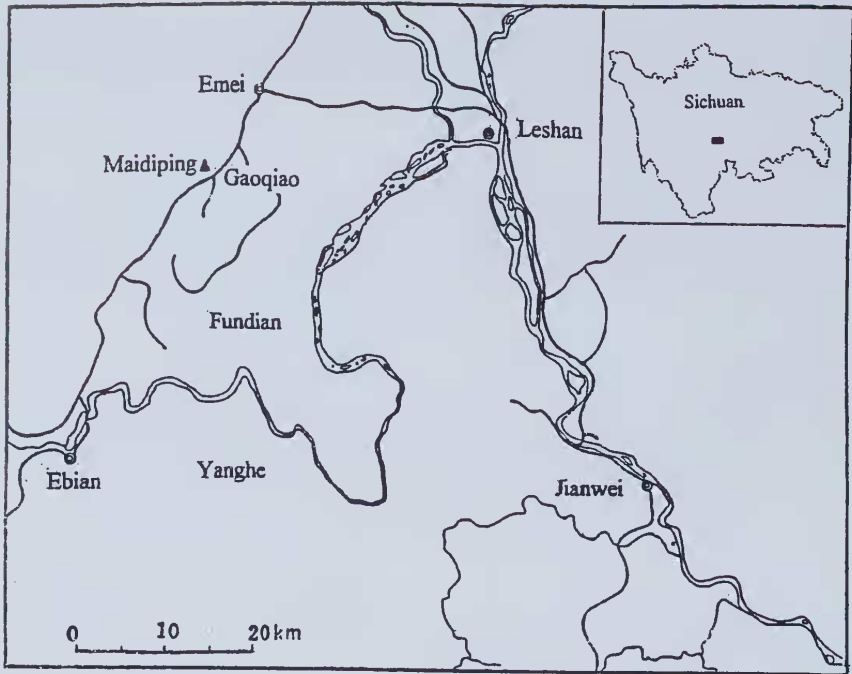


Figure 1 Sketch map showing the fossil locality.

This family was erected to include three genera: *Archaeotremaria* Yu, 1979 from the Lower Cambrian Maidiping Member of Hongchunping Formation in western Sichuan, *Granoconus* Yu, 1979 from the Lower Cambrian Huangshandong Member of Tongying Formation in western Hubei, China and *Rozanoviella* Missarzhevsky, 1981 from the Lower Cambrian Tommotian to Atdabanian Stages of western Mongolia.

Genus *Archaeotremaria* Yu, 1979 emend.

Archaeotremaria Yu, 1979: 249, 264; Dzik, 1981: 119; Yu, 1983: 1572; 1987a: 55; 1987b: 170; 1990: 144; 1996: 211.

Type species

Archaeotremaria polytremata Yu, 1979: 249, 264, by original designation, from Lower Cambrian Maidiping Member of Hongchunping Formation, at Maidiping of Emei, Sichuan, China.

Diagnosis

Minute, patelliform, bilaterally symmetrical. Protoconch unknown. Apex obtusely rounded. Dorsum broadly rounded with an obtuse dorsal ridge in the central part, a series of tremata on the tubular projections on the median dorsal ridge, the tremata divided into two small pores, which were

gradually filled with shell secretion during growth, the last one remaining open and serving as an exhalant function. Aperture large, expanded, subelliptical in form. Surface ornamented with concentric, periodic rugae, growth lines and pustules. Muscle scars unknown.

Remarks

In the presence of the tremata on the tubular projections on the median dorsal ridge and ornamentation of numerous small pustules, this genus resembles *Granoconus* Yu, 1979 from the Lower Cambrian Huangshandong Member of Tongying Formation of the Hujintan section of Yichang, Hubei (Yu, 1979: 250, 265; 1987b: 173; 1990: 145). However, *Granoconus* has a cyrtconic shell, a comparatively narrow dorsal ridge and the trema is a single pore.

The general form of the shell and the presence of a series of tremata in the central part of the dorsum, suggests comparison with *Rozanoviella* Missarzhevsky, 1981 from the Lower Cambrian Tommotian to Atdabanian Stages of western Mongolia (Missarzhevsky, 1981: 27; Zhegallo, in Voronin *et al.* 1982: 46; Zhegallo in Esakova and Zhegallo, 1996: 164), but in *Archaeotremaria* the shell has larger and fewer tremata on the tubular projections, of which the last remains open. In *Rozanoviella*, the numerous small tremata on the median dorsal ridge are chain-like in appearance;

in *Archaeotremaria*, the tremata are divided into two small pores, whereas in *Rozaoviella* the trema is a single pore.

In *Archaeotremaria*, the presence of a series of median dorsal tremata is similar to the condition in the bellerophonitoidean gastropods *Tremanotus* Hall, 1865, both sharing such common features as: 1) bilaterally symmetrical shell, 2) the possession of a series of median dorsal tremata on the tubular projections, 3) the periodic rugae, and 4) an expanded aperture. However, there are still great differences between them, particularly in the shell being patelliform in *Archaeotremaria*, while the isostrophic form characterises *Tremanotus*. In *Archaeotremaria*, the tremata are divided into two small pores, whereas in *Tremanotus*, the tremata are a single pore. In the former, the apex is situated at the posterior part of the shell, but in the latter, the earliest whorl is succeeded by the later closely coiled ones.

In the general aspect of the tremata on tubular projections, *Archaeotremaria* somewhat resembles *Knightites* Moore, 1941 from Upper Pennsylvanian of Kansas. However, *Knightites* has an isotrophic shell, spiral ornament and projecting tubes on either side of the selenizone.

Archaeotremaria polytremata Yu
Figures 2 A-I; 3 A-D

Archaeotremaria polytremata Yu, 1979: 249, plate 4, figures 6-11, text-figure 6; 1987a: 55, plate 3 figures 3, 4; 1987b: 171, plate 33, figures 1-5; plate 34, figures 1-5, text-figures 21, 52; 1990: 162, plate 7, figures 1-3; 1993: 241, text-figure 23.

Material Examined

Holotype

NIGP 54460, in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. Collected by the writer in 1977 from the Lower Cambrian Maidiping Member of Hongchunping Formation at Maidiping of Emei, Sichuan, China.

Paratype

NIGP 54461 from same locality and horizon as the holotype.

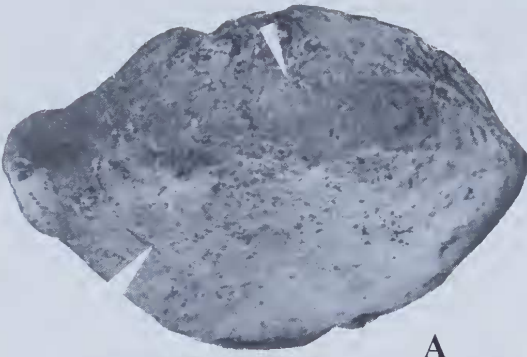
Description

Minute, patelliform, bilaterally symmetrical. Protoconch unknown. Apex bluntly rounded, slightly in posterior part of centre. Subapical area scarcely rounded and inclined to the posterior margin. Lateral slopes broadly rounded. Dorsal side broadly rounded, moderately convex, gradually sloping to the anterior margin, with an obtuse dorsal ridge in the central part of the dorsum, and a

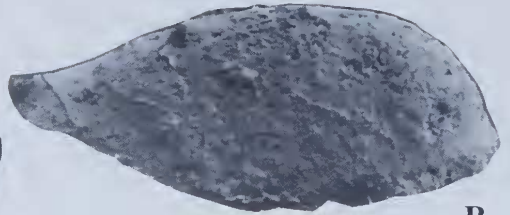
series of tremata on the median dorsal ridge. The earliest tremata unclear, about seven tremata can be observed on the mould, usually on the tubular projections. First trema very small and moderately protruding, closed by shell secretion, situated about one-third of the posterior margin from the shell. Second and third tremata small, subcircular, a little protruding and closed by shell secretion. The fourth trema strongly protruding, inclined forward, broadly rounded in the basal part, gradually tapering toward the top, situated at about one-third of the anterior margin from the shell, just on the periodic ruga and also closed. The fifth trema slightly protruding, poral margin slightly broken, but the general form and periodic ruga can be seen. The poral wall of the sixth trema broken, remaining a subcircular pore. Pore small, situated between the middle part of the two periodic rugae. The last one is the highest and biggest one in the series of tremata, subelliptical in plan view. Poral wall thickened, upper part of poral wall a little convexly arched first, then gradually, concavely inclined and extending downward, forming a V-shaped septum, dividing the trema into two small pores; pore subreniform in outline and equal in size, located near the anterior margin, and serving as an exhalant function.

Surface ornamentation of the shell is not preserved, although some regularly distributed periodic rugae are still visible on the apical area, and sub-apical area, especially the latter, where at least five periodic growth rugae can be seen on the anterior part of the dorsum (Fig. 3A). The inner periodic growth ruga is complete, forming a ring on the dorsum, situated behind the second trema. The second and third periodic growth rugae are similar morphologically to the inner one, located behind the third and fourth tremata. The fourth and fifth periodic growth rugae are not well preserved due to the periphery of the shell being slightly broken. Aperture large, occupying most of the ventral side, subelliptical in shape, posterior margin narrowly rounded, lateral sides broadly arcuated, anterior margin not known in detail.

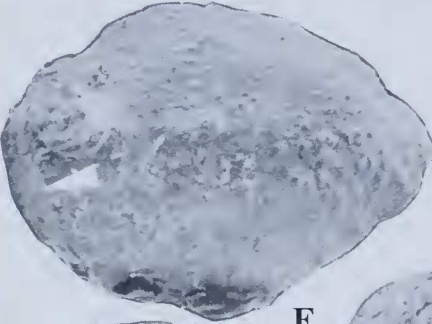
The paratype, shown in Figures 2E-I, 3C-D, is a well preserved internal mould. It is very small, possibly a juvenile. In plan view, the shell is elliptical in shape. Dorsal side strongly arched, broadly rounded, gradually sloping to anterior margin. Posterior margin narrowly rounded, lateral slopes gently arcuated. The centre of the shell has an obtuse dorsal ridge, with four tremata on tubular projections. First two tremata very small, scarcely projecting, located near the apical area. Third trema distinctly protruding and inclined forward, broadly rounded in the basal part, slowly constricted to the top; poral wall thin and subelliptical in shape, narrowly rounded posteriorly, broadly curved laterally, narrow anteriorly, divided into two small



A



B



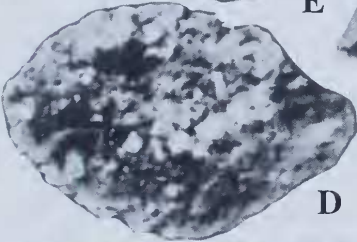
E



F



C



D



I



H



G

pores by a thin septum and closed by shell secretion. The last tremata is the largest and highest, strongly protruding and slightly inclined forward; poral opening circular in plane view, slightly flared and reflected, the anterior part seems to extend a little forward (Figure 2F); nearly heart-shaped in anterior view (Figures 2F–H, 3D). Posterior surface of poral wall is thickened, and a little swollen. Lateral parts slightly convex initially, middle part flatly concave, gradually sloping and extending downward, forming a "V" shaped septum dividing the opening trema into two small pores, which are equal in size and reinform in outline.

Surface ornamented with numerous small pustules, among which can be observed several rows of pustules that seem to correspond to periodic growth rugae. Muscle scars unknown.

Dimensions (mm)

	Length	Height	Width
NIGP 54460	1.500	0.546	1.000
NIGP 54461	0.588	0.210	0.448

Horizon and locality

Maidiping Member of Hongchunping Formation at Maidiping of Gaoqiao, Emei.

Discussion

In 1979, the writer established the family Archaeotremariidae Yu, 1979 within the Class Monoplacophora based on the genus *Archaeotremaria* Yu, 1979. In addition to the type genus, Yu (1987b) assigned *Granoconus* Yu, 1979 from the Lower Cambrian Huangshandong Member of the Tongying Formation of Yichang, Hubei, China and *Rozanoviella* Missarzhevsky, 1981 from the Lower Cambrian Tommotian to Atdabanian Stages of western Mongolia to this family. Nevertheless, he pointed out that *Archaeotremaria* possessed a row of tremata on the tubular projections on the dorsal ridge that differed from the all known genera in the Monoplacophora (Yu, 1979: 249). The term Class Monoplacophora was abandoned by Peel (1991), who proposed using the Class Tergomya, Horny 1965, for forms possessing a bilaterally symmetrical exogastric shell with bilaterally symmetrical muscle scars (Peel, 1991a; Berg-Madsen and Peel, 1994; Yochelson, 1994; Horny'

and Peel, 1996; Webers and Yochelson, 1999; Yu and Yochelson, 1999).

The species *Archaeotremaria polytremata* is very small. The very small size (about 1–2 mm) of the Early Cambrian molluscs has been discussed in detail by many scholars (Runnegar and Jell, 1976; Runnegar and Pojeta, 1985; Chaffee and Lindberg 1986; Salvini-Plawen, 1990; Dzik, 1991; Peel, 1991; Haszprunar, 1992). The holotype of *A. polytremata* is 1.500 mm in length, with seven tremata on the dorsal ridge. The paratype is a juvenile 0.588 mm long, with four tremata.

The molluscan character of this species taxon is shown the following combination of characters: bilaterally symmetrical, patelliform shape, with apex located slightly posterior of centre; aperture ventral; dorsal side broadly rounded, the tremata series marked by tubular projections along the median dorsal ridge, which were infilled sequentially with shell growth. The last of these remained open, serving the exhalant function. At least five periodic growth-rugae can be seen on the dorsal side of the internal mould.

Among the Early Paleozoic molluscan fauna, there are a few genera of bellerophontoidean gastropods which have one or more tremata on the median dorsal side, such as the Lower Cambrian *Granoconus trematus* Yu, 1979 (Yu, 1979, plate III, figures 33–35, text-figure 7; 1987b, plate 33, figures 6–9, text-figure 53; Figure 3E–3F), *Rozanoviella atypica* Missarzhevsky, 1981 (Missarzhevsky 1981, plate III, figure 9, text-figure 2; Zhegallo in Voronin *et al.*, 1982, plate I, figures 10–11; Zhegallo in Esakova and Zhegallo 1996, plate XX, figures 4–5; Figure 3G–3I); the Middle Ordovician-Silurian *Tremanotus* Hall, 1865, (Lindström, 1884; Knight, 1941; Knight *et al.*, 1960; Horny', 1963; Yochelson, 1967; Peel, 1972, 1991b) and *Salpingostoma* Roemer, 1876 (Lindström, 1884; Knight, 1941, 1952; Knight *et al.*, 1960; Peel, 1991b). Nevertheless, so far as I am aware, no monoplacophoran or tergomyan has dorsal tremata.

It is worth noting that *A. polytremata*, not only has a series of tremata on tubular projections from the apex to the anterior margin on the median dorsal side, but there also seems to be a periodicity in its formation. With the growth of the shell, the previously formed trema is gradually filled with shelly substance and then subsequently a new trema develops, remaining open and serving as an exhalant outlet. It can be demonstrated that the tremata develop throughout

Figure 2 A–I, *Archaeotremaria polytremata* Yu. A–D, holotype NIGP 54460. A, dorsal view, showing seven tremata on the median dorsal ridge from the apex to anterior margin and some concentric, periodic growth rugae (arrow), x 55. B, left lateral view, x 50. C, right lateral view, x 36. D, apertural view, x 40. E–I, paratype NIGP 54461. E, oblique dorsal view, showing four tremata on tubular projections on the median dorsal ridge and some traces of concentric, periodic growth rugae (arrow), x 120. F, dorsal view, showing the tremata and sculpture, x 180. G–H, enlargement of the last two tremata and sculpture, showing the tremata are divided into two small pores by a V-shaped septum, x 200 and x 300. I, right lateral view, showing four narrow bands, x 120.

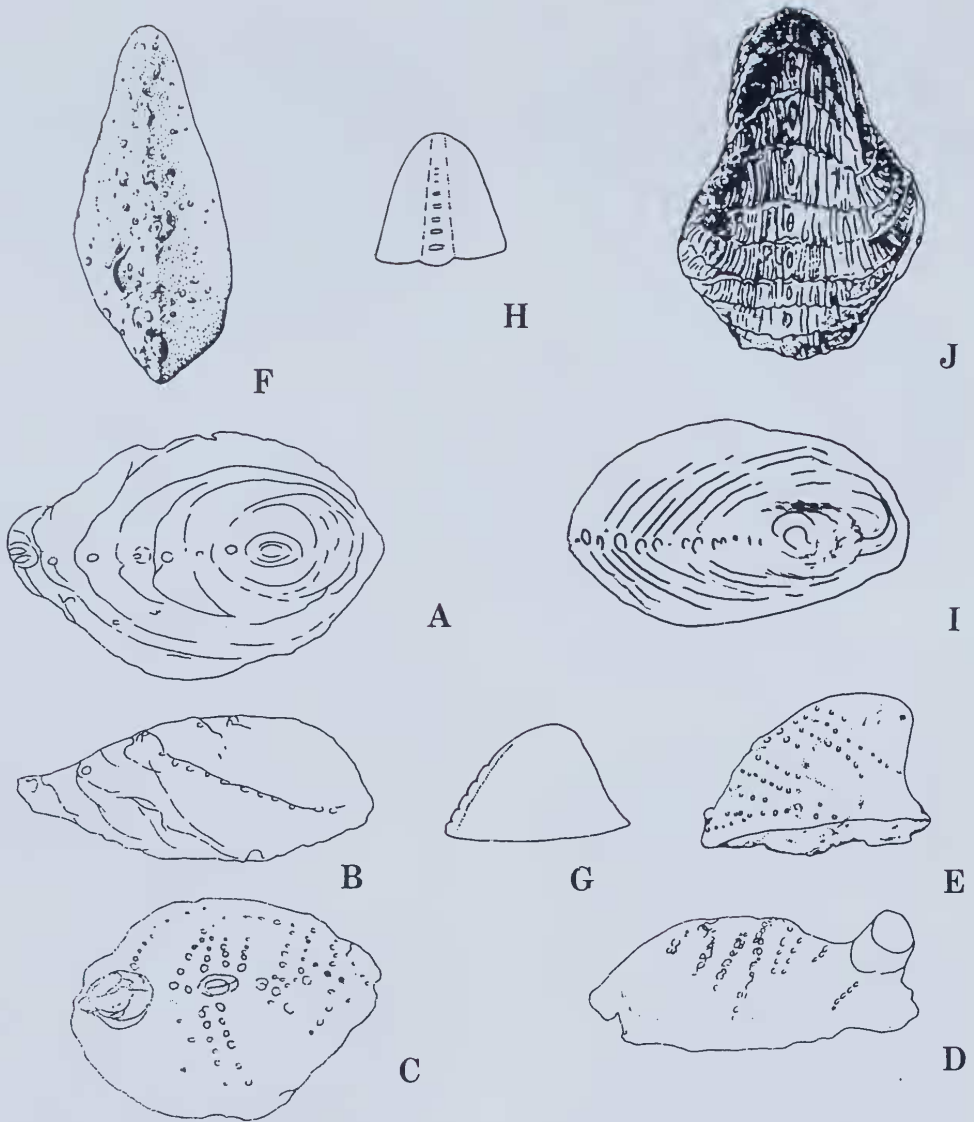


Figure 3 A-D, *Archaeotremaria polytremata* Yu. A-B, holotype NIGP 54460. A, dorsal view, showing tremata and concentric, periodic growth rugae, x 38.5. B, left lateral view, showing tremata on the tubular projections, x 35. C-D, paratype NIGP 54461. C, dorsal view, showing the tremata and some pustules, x 85. D, right lateral view, showing four narrow bands, x 85. E-F, *Granoconus trematus* Yu, holotype NIGP 54455. E, left lateral view, showing tremata on the tubular projections x32. F, anterior view, x 42. Lower Cambrian of Hubei, China (after Yu Wen, 1979). G-I, *Rozanoviella atypica* Missarzhevsky, G, left lateral view, x 30. H, anterior view, x 30. Lower Cambrian of western Mongolia. (after Missarzhevsky, 1981). I, dorsal view, x 55. Lower Cambrian of western Mongolia (after Zhegallo in Voronin *et al.*, 1982). J, *Tremnanotus longitudinalis* Lindstrom. dorsal view, x 1. Middle Silurian of Gotland, Sweden, (after Lindström, 1884).

ontogeny in *Archaeotremaria*. The tremata of *A. polytremata* are divided into two small pores, indicating that *Archaeotremaria* may be a gastropod having paired tentacles. However, the living monoplacophoran *Neopilina galathea* Lemche (1957, figures 1-4) and *Vema ewingi* Clarke and Menzies

(1959, figures 1-2) have five and six pairs of gills respectively. *Pilina liaoningensis* Yu and Yochelson (1999, figures 2a, 2b, 3f, 3g, 4a, 4b) from the Upper Cambrian Wanwankou Member of Fengshan Formation of Liaoning, China has five pairs of scars of the gill cavity.

The form of the tremata and their presumed function in *Archaeotremaria* are very similar to those of the Middle Ordovician *Tremanotus* Hall, 1965. Though distant from each other in absolute geologic time, such gaps within plausible or speculative lineages are not unusual in view of our far from complete knowledge of Early Paleozoic molluscs. Ongoing new discoveries and research can be expected to close some of the gaps separating Early Cambrian and Middle Ordovician trematose molluscs. It has long been argued that bellerophontids are most similar to pleurotomarians (Meek, 1866; Lindström, 1884; Ulrich and Scofield, 1897). During the last fifty years, there have been many contributions concerning similarities between bellerophontoidean gastropods and pleurotomarians (Knight, 1947, 1952; Knight *et al.* 1960; Yochelson, 1967, 1984; Peel, 1972, 1991b; Batten, 1975; Golikov and Starobogatov, 1975; Linsley, 1978; McLean, 1984). The appearance of the primitive patelliform *Archaeotremaria* in the Early Cambrian, may provide some evidence for further discussion on the relationship between the bellerophontoidean gastropods and the pleurotomarians. Moreover, the presence of regularly distributed periodic rugae is another noteworthy feature in this genus; at least five concentric, periodic growth rugae can be seen on the internal mould, periodically spaced, usually between the tremata. This character is similar to that of *Tremanotus portlocki* Reed (1920–1921, plate XIII, figure 4) from the Ordovician of Tyrone, United Kingdom, *Tremanotus longitudinalis* Lindström (1884, plate III, figures 39–40; plate IV, figures 5, 6; Figure 3J) from the Lower Silurian of Gotland, Sweden and of *Tremanotus tuboides* Perner (1903, plate 82, figures 11–15, text-figure 88; Horny', 1963, plate XVIII, figures 1–5) from the Middle Silurian Wenlockian Stage of Central Bohemia. Therefore, *Archaeotremaria* is quite different from tergomyans, but closely resembles certain gastropods.

Furthermore, the most important distinguishing feature of *Archaeotremaria* is that the surface of the internal mould bears numerous small pustules, especially on the right side of the paratype (NIGP 54461), where there are four narrow bands, from the median dorsal side, extending slightly backward. Previously Yu regarded these narrow bands as muscle scars in the inner surface (Yu, 1987a, plate 3, figures 3–4; 1987b, plate 34, figures 1–5, Text figure 52; 1990, plate 7, figures 1–3; 1993, Text-figure 23). After re-examination of the holotype and the paratype of the type species, I consider that four pairs of muscle scars do not exist. The interior of the shell in the Class Tergomya is characterised by bilaterally symmetrical muscle scars on the bilaterally symmetrical shell.

In summary, it has been shown that *Archaeotremaria* has a patelliform shell with a series

of median dorsal tremata and periodic growth rugae. This combination of characters clearly indicate that *Archaeotremaria polytremata* is a primitive patelliform gastropod rather than Tergomya.

ACKNOWLEDGEMENTS

I would like to take this opportunity to thank K.J. McNamara and G.W. Kendrick, Western Australian Museum and two anonymous reviewers. Thanks also to Danielle West and Anne Nevin for their technical assistance.

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